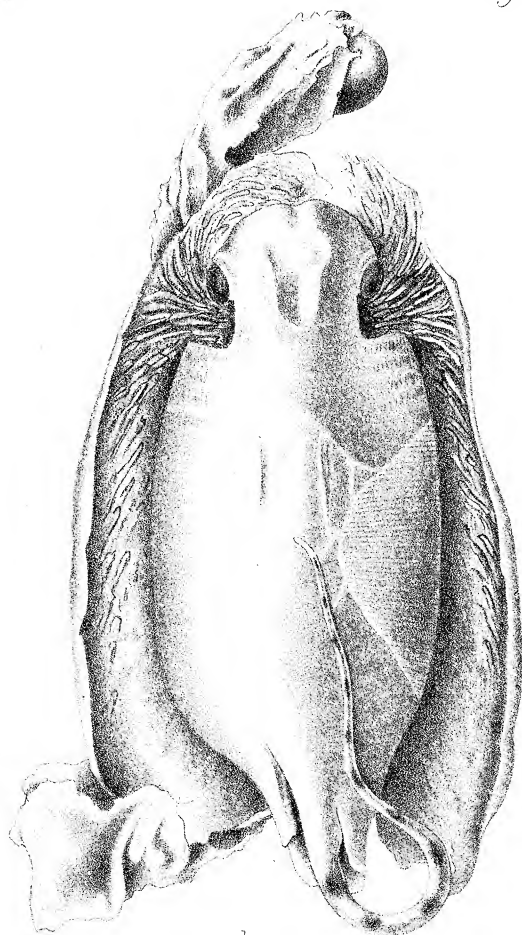
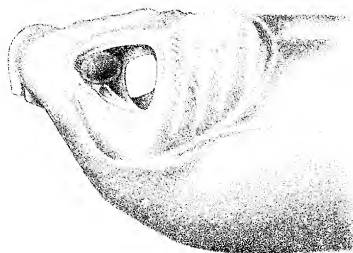




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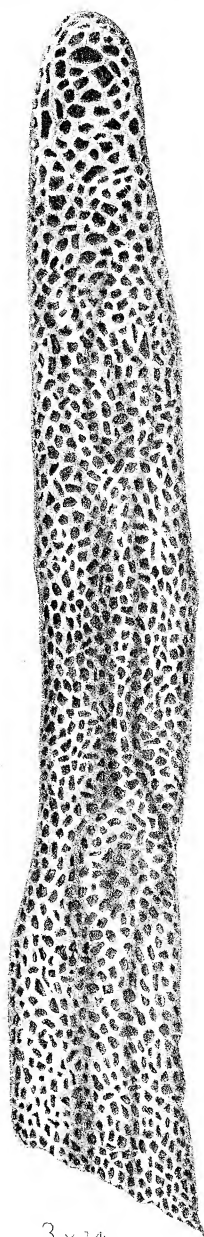
PTEROPLATEA MICRURA.

EXPLANATION OF PLATE 7.

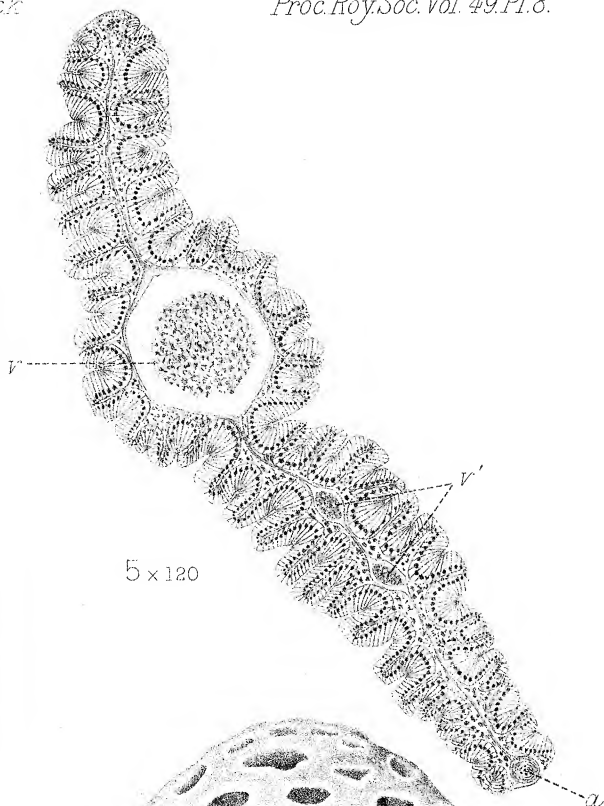
- Fig. 1. Gravid uterus of *Pteroplatea micrura*, opened by a longitudinal incision in its dorsal wall, with the flaps turned back, so as to show the passage of the large bundles of trophonemata through the spiracles into the pharyngeal cavity of a single fœtus.
- Fig. 2. Head and shoulders of the same fœtus from the left side, to show the great size and the lateral position of the spiracles.

EXPLANATION OF PLATE 8.

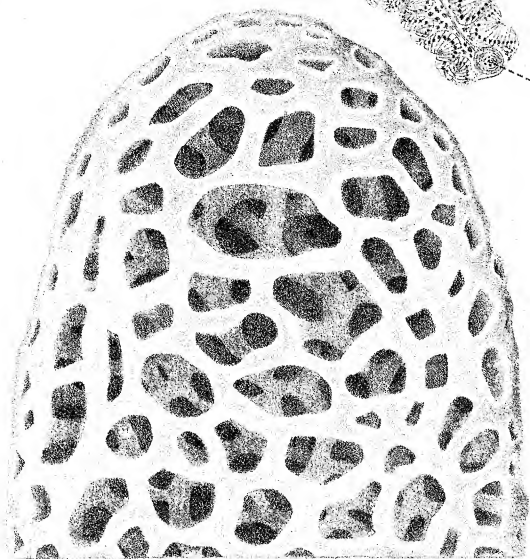
- Fig. 3. Distal moiety of a large trophonema from one of the spiracles, to show the superficial texture and the outstanding vein. $\times 14$.
- Fig. 4. Apex of the same trophonema, to show the compound duct-openings. $\times 66$.
- Fig. 5. Transverse section of a trophonema in its distal half, to show the glands in vertical section. $\times 120$. α , artery; V , main trunk; and V', V' , branches of vein with coagula in their lumina.



3 x 14



5 x 120



4 x 66

PTEROPLATÆA MICRURA.

March 19, 1891.

Mr. JOHN EVANS, D.C.L., LL.D., Treasurer and Vice-President,
in the Chair.

The Right Hon. Lord Hannen was admitted into the Society.

The Presents received were laid on the table, and thanks ordered
for them.

The following Papers were read :—

- I. “On the Uterine Villiform Pápillæ of *Pteroplatea micrura*,
and their Relation to the Embryo, being Natural History
Notes from H.M. Indian Marine Survey Steamer ‘Investigator,’
Commander R. F. Hoskyn, R.N., Commanding. No. 22.” By
J. WOOD-MASON, Superintendent of the Indian Museum and
Professor of Comparative Anatomy in the Medical College of
Bengal, and A. ALCOCK, M.B., Surgeon, I.M.S., Surgeon-Naturalist
to the Survey. Communicated by Professor M. FOSTER, Sec. R.S.
Received February 24, 1891.

Contents.

- § 1. Preliminary Historical Sketch.
§ 2. Recent Observations on the Uterine Villi of some Indian Rays.
§ 3. The Uterus and Embryo of *Pteroplatea micrura*, and the Relation of the
Uterine Villiform Papillæ (or Trophonemata) to the Embryo.

§ 1. *Preliminary Historical Sketch.*

That in the females of several Selachioids and Batoids the mucous
membrane of the terminal portion of the oviduct, or uterus, is pro-
vided with glandular structures which secrete an albuminous fluid
destined in some way or other for the nourishment of the developing
embryo is a bionomic phenomenon which has attracted the attention
of numerous physiologists and histologists, though, as far as we are
aware, it has never been fully followed out.

Concerning the intra-uterine arrangements for the protection and
nutrition of the egg or embryo among Selachians, Gegenbaur
(‘Grundzüge der Vergleich. Anat.,’ p. 875) writes :—“The terminal
division of the oviduct of the Selachians, which has already been
mentioned as functioning as uterus, also differs from the rest of the

oviduct in the nature of the mucous membrane. In many it is raised into villi. Glands are much developed. The relation of this division of the oviduct to the egg or to the embryo that originates therefrom is a tolerably various one. Least intimate is it in the oviparous Selachii (*Raja* and *Scyllium*): only furnishing the egg-case. In others (*Spinax*, *Acanthias*, *Scymnus*), a shell is also developed, but only for a short time, and the embryo afterwards lies free in the uterus. Here come those Selachians in which there is no longer any shell at all developed, and from this circumstance results the nutritive connexion of the fœtus with the uterine wall by the intermediation of the yolk-sac."

This passage, although it clearly defines the well-known functions of the Selachian uterine mucosa, on the one hand of secreting an egg-case, and on the other hand of forming a vascular nutritive connexion with the modified yolk-sac of the embryo, makes only a vague allusion to another modification of function: namely, the secretion by special uterine glands of a nutritive fluid which might be absorbed or ingested by the developing embryo.

Leydig also ('Handbuch der Histologie,' Ed. 1857, p. 517) describes the vascular uterine villi of *Acanthias*, *Spinax*, *Scymnus*, and *Trygon*, though without discussing their relation to the egg or to the embryo. He says:—"In the Selachians the mucous membrane (of the uterus) either appears smooth and possessing only zig-zag longitudinal folds (*Scyllium*, for example), or it bears much-developed villi (*Acanthias vulgaris*, *Spinax niger*, *Scymnus lichia*, *Trygon pastinaca*). These villi are placed sometimes (*Acanthias vulgaris*, *Scymnus lichia*) in very regular longitudinal rows which cease towards the end of the uterus, and pass into leaf-like longitudinal folds; or, as in *Trygon pastinaca*, they are so crowded together that nothing more of the rest of the mucous membrane of the uterus appears. The villi possess an exceedingly rich vascular supply: there are to be distinguished in them at most two stronger vessels which interlace and run into one another at the end of the villus, and between the two a close-meshed vascular network. These vessels are in the gravid uterus distinguished by a proportionately very thick circular muscular layer." There are figures (p. 318, Ed. 1857) of "the uterus of *Trygon*, opened, in order to show the villi"; and of "a bit of the uterine mucosa of *Spinax*, somewhat more than the natural size," showing the much-developed villi, which are represented as two- to three-branched.

The great comparative anatomist Johannes Müller, in his exhaustive paper: "Ueber den glatten Hai des Aristoteles" ('Abhand. Ak. Wiss. Berlin,' 1840, p. 188), reviews more completely the state of knowledge up to that date of the Selachian uterine structures which, quite apart from the secretion of egg-coverings or the formation of yolk-sac placentaë, are concerned in the elaboration of secretions

which are to be considered either as providing nourishment for the growing embryo after the nutritive yolk of the egg has been absorbed, or as maintaining and increasing the nutritive material of the yolk.

Of *Spinax niger* he says (*loc. cit.*, p. 236):—"The fœtus in the uterus is distinguished by possessing no trace of an egg-shell, and by the inner membrane of the uterus being beset by very long (six to eight lines long) filiform villi."

More particularly of the genus *Torpedo* he writes (*loc. cit.*, p. 239):—"The eggs possess no trace of shell membrane; they are only surrounded by an albuminous uterine fluid, as already Redi, Stenonis, Lorenzini, and in more recent times J. Davy, observed. Cavolini states that the yolk sticks to the walls of the uterus, and that this is effected by an innumerable crowd of red uterine glands lying on the yolk. By this are clearly meant the papilliform villi on the uterus of *Torpedo oculata*; but the yolk-sac in no way adheres to the uterus, as the observations of J. Davy show, observations with which what I myself have seen in the gravid uterus sent by Dr. Peters accords. The yolk-sac of the *Torpedos* is perfectly smooth. I can confirm the extraordinary difference observed by T. Davy in the structure of the mucous membrane of the uterus, which in *Torpedo oculata* is furnished with villi, in *Torpedo marmorata* with parallel longitudinal folds." Johannes Müller also quotes Davy's observations on the increase in weight, from the undifferentiated egg-stage to the completed fœtal stage, in *Torpedo*, notwithstanding the disappearance of the external yolk and the absence of any vascular maternal connexion.

Of the Spinacoid Shark *Scymnus lichia* he observes (*loc. cit.*, p. 237):—"In the fresh uterus, the fœtus and yolk-sac are surrounded by a white-of-egg-like fluid. Also in this Shark no trace of an egg-shell membrane is met with. The fœtus with its enormous yolk-sac is immediately surrounded by the uterus. The whole oval yolk-sac is, in the younger and middle stages of development, 4 inches long and 2 inches thick. The inner membrane of the uterus is furnished with cylindrical villi six lines in length."

John Davy ('Phil. Trans.,' 1834, pp. 531—540), in the research on the embryology of *Torpedo*, referred to by Johannes Müller, describes the mucosa of the gravid uterus of this Batoid, and specially dwells upon the absence of any vascular connexion between the embryo and the mother.

He states that, in several series of observations, while the average weight of undifferentiated eggs was 182 grains, and the average weight of eggs in which the embryo had appeared was 177 grains, the average weight of "ripe fœtuses" was 479 grains; and he asks how, in the absence of any sort of structural connexion between the fœtus and the mother, this remarkable increase of weight is to be explained.

He observed that there was to be found in the uterine cavity "a little fluid, generally milky, more rarely glairy, and sometimes bloody, which, on evaporation, yielded crystals of common salt, and a very little animal matter composed chiefly of albumen;" and he speculated on the possibility of this uterine secretion being nutritive. He negatived, however, the supposition that the embryo *in utero* could take in food by the mouth, and inclined, finally, to the opinion that the embryo increases by absorption, partly through the general surface of the body and partly through the branchial filaments.

Sir Everard Home ('Phil. Trans.,' 1810, p. 208), in a paper on the "Mode of Breeding of the Oviviviparous Shark," which is quoted by Joh. Müller, described the naked-eye anatomy of the oviduct of *Acanthias vulgaris*, the jelly and which fills that part of its cavity and which functions as a uterus in this Selachian. He states that when the young one is completely formed the yolk remains attached to the belly by a long cord of blood-vessels, and that the young one in this state "swims" in the uterine jelly. The jelly he regards as a secretion of the oviduct.

Home further quotes the observation of Dr. Patrick Russell, that a Shark caught in lat. 70° N. had the oviducts distended with young ones, each with the yolk-sac attached; the young ones swimming in a "white gelatinous liquid, thicker than the liquor amnios of Quadrupeds." Home supposed that the function of the jelly was to aerate the foetal blood.

To sum up, we find that in *Spinax niger*, *Scymnus lichia*, *Acanthias vulgaris*, *Trygon pastinaca*, *Torpedo oculata* (and also in *Myliobatis noctula* and *Centrina salviani*, according to Trois, in a paper in the 'Atti del Istituto Veneto,' vol. 2, which we have unfortunately been unable to obtain), special glandular villi have been observed on the uterine mucosa, which villi have in some cases been supposed to bear, either to the egg or to the developing embryo, some relation of support or nutrition other than that of furnishing an egg-case, or of assisting in the formation of a vascular connexion (yolk-sac placenta) between the embryo and the mother.

In *Scymnus lichia*, on the one hand, it seems certain, from Müller's researches, that the villi secrete a fluid which nourishes the embryo through the medium of the yolk-sac; while in *Torpedo*, on the other hand, it is certain that, at least in the later stages, the secretion reaches the embryo in some less indirect manner, and the question has actually been asked whether it is ingested by the embryo.

In corroborating the opinion as to the function of the villi of the Selachian uterine mucosa, we are able to bring evidence of a case in which the nutritive secretion is actually conveyed into the pharynx of the embryo.

Following on this, and because the term "villus," in its connexions

with mammalian physiology, has come to connote a structure which essentially absorbs nutriment, we propose to term the villiform structures of the uterine mucous membrane in Selachians, which essentially secrete nutriment, *trophonemata*; and by this name they will be referred to in the descriptive portion of this paper.

§ 2. *Recent Observations on the Uterine Villi of some Indian Rays.*

In the 'Journal of the Asiatic Society of Bengal,' vol. 59, Part II, p. 51, the second-named contributor of this paper described some observations on the uteri and the gestation of *Trygon bleekeri* and *Myliobatis nieuhofii*, which it is necessary here to briefly recapitulate.

In a large female of *Trygon bleekeri*, taken on the 15th December, 1888, in the Máhánaddi estuary, the distal end of the right oviduct was found to be enormously dilated, and to contain in its cavity a fully-developed male foetus with a disk $11\frac{3}{4}$ inches long and $10\frac{3}{4}$ inches broad. The folded foetus lay free in the uterine cavity, quite destitute of membranous covering, without any structural connexion with the mother, and without any vestige of external yolk-sac. The uterine mucous membrane, which was a vivid vascular scarlet, such as in Fishes is usually seen in the gill-laminæ only, was covered with an abundant highly-albuminous fluid, secreted by a crowded layer of glandular filamentous villi which formed the inner coat; and it was inferred that this secretion was a uterine milk elaborated for the nourishment of the embryo. In the absence of any special absorbent organs, and because the embryo was so folded that any supposed "absorbent function" of the skin would have been as much as possible limited, it was further inferred that the "milk" was taken in by the embryo by the mouth; though unfortunately the foetal stomach was not examined until *post-mortem* changes were advanced. It may be mentioned that the foetus did not possess branchial filaments.

Again, in *Myliobatis nieuhofii*, the structure of the uterine glands has been made out, but we have had no opportunity of ascertaining their relation to the egg or to the embryo. In an adult female, taken off the Godáviri Delta on the 31st March, 1889, the left ovary was found to be full of enlarged ova, while the distal end of the oviduct formed a globular swelling with thick, muscular walls, and a mucous membrane thickly beset with long foliaceous villi. The entire surface of the mucous membrane, both villous and inter-villous, was found to consist of a close-set aggregation of tubular glands, most of which were simple follicles resembling the Lieberkühnian follicles of human anatomy, though at the periphery of a villus they are commonly racemose.

We have now, in the case of *Pteroplatea micrura*, discovered

another instance of a Batoid which develops a naked embryo in an uterus with a mucous membrane of a complex structure; and while the histological characters of portions of the uterine mucosa are those of a secretory gland, the disposition of these glandular portions is such as to leave no doubt that the greater part of their secretion is poured into the pharynx of the embryo as it lies in the uterus.

§ 3. *The Uterus and Embryo of Pteroplatea micrura; and the Relation of the Uterine Villiform Papillae (Trophonemata) to the Embryo.*

In December, 1889, the detached pregnant uterus, with part of one oviduct and kidney, of a Ray which had been captured in the estuary of the Hooghly was sent to the Indian Museum by Mr. A. J. Milner, of the Bengal Pilot Service.

The embryo, after removal, was identified as *Pteroplatea micrura* (Bl. Schn.). The measurements of its disk are, length 3·4 inches, breadth 6·5 inches; its caudal spine is not yet developed, and the nasal valves are still separate; its liver is of very large relative size, and the intestine is greatly distended with grumous bile-stained material.

The gravid uterus forms a symmetrical ovoid swelling; dorsally its wall is almost membranous, ventrally it is still thin; laterally, and especially antero-laterally, it is thick and muscular.

Internally, it is lined with mucous membrane, which, dorsally and postero-laterally, is quite smooth.

On the ventral aspect, however, the mucous membrane begins to be extended in the form of short, compressed papillae, and these, anteriorly and laterally, grow by degrees longer and more numerous, until, at a point in the antero-lateral part of the uterus which coincides with the position of the spiracle of the embryo *in situ*, they form on each side a large bunch of long-compressed villiform trophonemata, the histological structure of which will be presently described.

On opening the pregnant uterus by a dorsal longitudinal incision, the naked embryo is found lying prone, head forwards, and tightly rolled in a right-to-left spiral. Although the embryo is in uniform close contact with the uterine walls, there is no sort of structural connexion between it and the mother, and no trace of any such previous connexion: nor can any vestige of external yolk-sac be observed. But by the rolling up of the embryo the spiracles, which are large patent cavities communicating freely with each other and with the pharynx, and smooth-walled, except for a very faint pectination anteriorly, come to have a lateral position, and deep into them passes, on each side, the lateral bunch of long trophonemata above mentioned, in such a way that the secretion of these richly-glandular

trophonemata can only pass down the pharynx of the embryo. The only other external communications of the pharynx, namely, the mouth and gill-clefts, are firmly closed, the opposite margins of the external gill-clefts being in the most complete apposition. There are, consequently, no branchial filaments.

The trophonemata are narrow, strap-shaped processes of the uterine mucosa which widen very slightly and gradually from their base to about the middle of their length, whence they taper still more gradually to their rounded apex. Those which enter the pharyngeal cavity of the foetus are the longest of all, measuring from 18 to 20 mm. in length and about 1.4 mm. in extreme breadth. Save for the presence of a blunt thickening that traverses them in a somewhat sinuous course from base nearly to apex, tapering and branching as it goes, and standing out in fairly bold relief from both their surfaces, they appear quite flat.

Stained in borax-carminé, mounted in spirit, and viewed under a low power by reflected light, they present a minute, honey-combed appearance of their surfaces due to the presence of innumerable small depressions. From the appressed conjunction of ridges which bound these, a slightly elevated polygonal network results.

Transverse sections of a trophonema shew that these depressions are the funnel-shaped mouths, narrowing below into the lumina, of small, short, bulb-shaped glands of the same simple tubular type as is seen, for example, in the crypts of Lieberkühn, or, better still, in the gastric glands of anthropotomy.

The glands are arranged perpendicular to the surface, side by side, in the substance of the mucosa—into which they are, in fact, so many involutions of the investing epithelium—so that the bases of those of opposite sides are separated from one another only by blood vessels and a very meagre, if any, connective tissue.

Vertical sections of a trophonema in planes parallel to its surface, or, in other words, transverse sections of groups of glands, shew that these are so closely packed as to be polyhedral by appression.

For a certain distance from the base of the trophonemata the depressions are small and simple, but they soon become larger and compound, each being then the common mouth or short duct of a little group of glands, just as in the human stomach, where one meets with simple glands, each with its independent opening, and with groups of glands opening into a common depression of the mucous surface.

The larger (secondary) depressions, it is obvious from an attentive study of the surfaces of several trophonemata, as well as from transverse sections, have resulted from the further depression of the smaller (primary) depressions in groups; and the raised margins of the former result from the coalescence of those portions of the margins

of the latter which are not involved in the general secondary depression.

The epithelium is very thick in the bulbous basal portion of the glands: here its constituent cells are very long, taper from basement membrane to lumen, and are arranged round an axial cell in the form of a cone, of which the outer cells do not extend far up the sides of the gland. Above this the cells become gradually shorter and less oblique, until at or near the mouth they pass into an ordinary columnar epithelium resting perpendicularly on the basal membrane.

The nucleus of the cells is oval, and stains very strongly. It lies excentrically near the base of the cell, which stains only less strongly than the nucleus itself, so as to form a sharply-defined, coloured basal stratum, in which the nuclei are included, throughout the gland. This deeply-stained band is most conspicuous in the basal cells, which are arranged in the form of a cone, and perhaps constitute the chief, if not the only, seat of active secretion.

Not a single cell in any of the sections has been observed to have undergone mucoid degeneration; but many have been noticed to contain minute globules, probably of secretion, not only in the coloured basal portion, but also in the clear and unstained outer part of their protoplasm.

The sections shew coagulated secretion in the mouths and lumina of many of the glands. The glands measure 0·06 to 0·08 in length by 0·04 to 0·07 in breadth. In a trophonema, 12 mm. long by 1·4 mm. in uniform width throughout, taking 0·05 mm. as the average diameter of the glands, we have calculated that no less than 21,280 glands are present—a result which is probably not far from the mark either way. The trophonemata are exceedingly vascular. Two vessels are present in all: an artery, which runs in the substance of one of their margins, and a vein, which takes a sinuous course not quite along the middle, but nearer to the opposite margin, giving off in its course two or three short branches which may or may not anastomose with the main stem. Both vessels taper towards the apex, near to which they are resolved into a capillary plexus, or rather into a system of narrow sinuous cavities which establishes a communication between the two sets of vessels. The wall of these cavities is formed of a delicate, nucleated membrane answering to, and appearing in some part of almost every section to be in actual continuity with, the endothelial lining and subjacent intima of the vein, into which some of the sinuses can actually be observed to open occasionally.

The vein is much larger than the artery: its calibre in that part of its course across which the section has been taken being no less than five times as great. The artery is strongly contracted and empty: the vein, on the other hand, is fully dilated and filled with coagulated blood, even to its lateral branches and the larger of its

affluent sinuses. Hence in lightly-stained trophonemata, examined entire under a lower power, the artery is only just visible by trans-
 parence, while the vein presents itself as a very distinct, branched, and tapering dark streak.

The connecting system of sinuses occupies the plane between the layer of glands of opposite sides, sending off processes around the base or specially secreting portion of every gland.

The glandular epithelium possesses no connective tissue framework beyond a filmy nucleated gauze, shreds of which can be traced wherever vacuities occur between the bases of adjoining glands, the whole trophonema consisting, as has already been stated, almost entirely of epithelium and blood vessels.

Having already stated our conclusion as to the function of the trophonemata in *Trygon* and *Pteroplatea*, and having described the path taken by the secretion in the latter, it only remains to consider briefly how far other views of the manner of absorption by the embryo of the nutrient uterine milk might apply in the case of these two fishes. Whatever may be the case in the earlier stages, in the later stages, at any rate, branchial filaments do not absorb nutriment from the maternal wall, for branchial filaments do not then exist.

Again, absorption through the general surface of the body of the embryo can hardly be looked upon as the principal channel of supply, because the embryo, at least in its later stages, is so folded or rolled up as to leave as little extent of surface as possible available for absorption.

[*P.S.*, April 8, 1891.—Since the above was written and despatched, we have had the good fortune to obtain from amongst the contents of the fishermen's nets at Cocanada several pregnant females of *Pteroplatea micrura*. The examination of these specimens in the fresh state, while it confirms our description in its principal particulars, renders some modification of it necessary. (1.) The number of young may be as many as three in each uterus, both uteri being developed. (2.) The number of young may be two in each uterus. Our first qualification will therefore be, *Uterus well developed on both sides; each uterus may contain from one to three young ones*. Again, where two and three young ones exist, the trophonemata (which appear to be fairly well developed over the entire mucosa of the uterus) are specially long opposite to the spiracles of the young one, *into which they pass*. Apparently—and this will be our second qualification—in the early stages of gestation the trophonemata are equally well developed over the entire surface of the uterine mucosa, but by the pressure exerted by the growing embryo they become greatly atrophied, except on those spots where they can pass into the spiracles of the embryo, and here, perhaps by compensation, they become hypertrophied.]



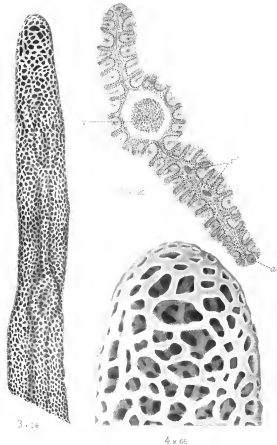
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PTEROPLATÆA MICRURA

EXPLANATION OF PLATE 7.

Fig. 1. Gravid uterus of *Pteroplatæa micrura*, opened by a longitudinal incision in its dorsal wall, with the flap turned back, so as to show the passage of the large bundles of trophocœmata through the spiracles into the pharyngeal cavity of a single fetus.

Fig. 2. Head and shoulders of the same fetus from the left side, to show the great size and the lateral position of the spiracles.



PTEROPODA MICRURA
EXPLANATION OF PLATE 8.

Fig. 3. Distal moiety of a large trophonema from one of the spiracles, to show the superficial texture and the outstanding vein. $\times 14$.

Fig. 4. Apex of the same trophonema, to show the compound dust-openings. $\times 66$.

Fig. 5. Transverse section of a trophonema in its distal half, to show the glands in vertical section. $\times 120$. α , artery; V , main trunk; and V' , V' , branches of vein with coagula in their lamina.